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NESTLING GROWTH AND DEVELOPMENT AND THE BREEDING ECOLOGY OF THE BEECHEY JAY

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Studies on the growth and development of young birds provide insight into ecological and social factors such as predation pressure, food supply, and amount and type of parental care that are important to a species during its reproductive cycle (Lack 1968; Ricklefs 1968, 1973, 1979; Case 1978). Studies of cooperatively breeding species are of particular interest because the assistance provided by nonbreeders may affect growth and development patterns (Bateman and Balda 1973, Woolfenden 1978). Many species of New World jays have been found to be highly social, cooperative breeders, but few studies have included a detailed analysis of their growth. Notable exceptions are studies by Bateman and Balda (1973) on Piñon Jays (*Gymnorhinus cyanocephalus*) and by Woolfenden (1978) on Florida Scrub Jays (*Aphelocoma c. coerulescens*).

We examined the growth and development of nestlings of the cooperatively breeding, sub-tropical Beechey Jay (*Cyanocorax* [*Cissilopha*] *beecheii*). We attempt to relate the growth pattern observed to certain ecological and social factors.

The ecology and breeding biology of this large jay of western México were examined by Raitt and Hardy (1979) and Raitt et al. (unpubl.) and are summarized below. Beechey Jays live year-round in groups of two to six individuals on 24–36-ha territories. Each group consists of a nucleus pair of breeders and a varying number of nonbreeding helpers, usually young of previous years that remain on their natal territory and occasionally birds that immigrate from nearby territories. All group members assist in building the nest, feeding and defending nestlings and fledglings, and defending the nest and territory. The breeding season begins with nest construction in mid-May and extends through mid-August, by which time all young are fledged. Groups attempt only one nest at a time and they stop after successful fledging. An unsuccessful first nesting attempt is generally followed by a second attempt. All incubation (18–19 days) and brooding are done by the breeding female. Clutch-size varies from three to five ($\bar{x}$ = 4.2) and brood-size from one to five ($\bar{x}$ = 3.2). The number of fledglings per group per year averages 2.3.

STUDY AREA AND METHODS

The results discussed herein are part of a 5-year (1974–1978) study on the ecology and breeding biology of Beechey Jays conducted near Mazatlán, Sinaloa, México (Raitt and Hardy

1979; Raitt et al., unpubl.). A description of the study site is given by Raitt and Hardy (1979). Weather data from the U.S. Department of Commerce (1965) for Mazatlán from 1951–1960 indicate that the winters are dry and mild (mean minimum for January and February = 7°C) and the summers are wet and hot (mean maximum for July–September = 30°C). The mean annual rainfall is 805 mm, but this is almost exclusively limited to a continuous 6-month period, producing two distinct seasons and "habitats" annually. From December to mid-June, when virtually no rain falls (0–<0.5 mm per month), the forest is almost totally barren of green foliage. This dry season is followed by a 2–3 week transition period, with fairly light, irregular rainstorms. The wet season, marked by heavy, almost daily storms, begins in mid- to late June and continues through late October, with July, August, and September each averaging over 200 mm of rain. Within 3 weeks after the rains begin, the trees and shrubs are fully foliated and a dense herbaceous understory develops.

This study extended from 28 May–30 July 1978. Six nests, belonging to five different groups, were found and each was visited daily until the young fledged (three nests), the nest was destroyed by predators (two nests), or the study ended (one nest). All but one nest had a complete clutch when discovered. The eggs from one nest were weighed to the nearest 0.5 g on the day of discovery, 12–13 days after laying.

Hatching of eggs within a clutch was slightly asynchronous, spanning as much as 24 h per nest. To permit individual recognition, each nestling was marked on the bottom of its toes with a combination of red and blue ink dots. After the nestlings were 1-day old (hatch day = day 0), each nest was visited daily between 16:30 and 19:00. Weight to the nearest 0.5 g and the lengths of all right primaries and rectrices to the nearest 0.5 mm were measured daily for each nestling. As they are exemplary of the feather growth observed, lengths of only primary 9 and rectrix 1 are discussed. Morphological and behavioral changes were noted for each nestling. All observations and measurements were made on the ground a few meters from the nest.

The six nestlings that survived to fledging were used for most of the final analyses of growth and development. Three nestlings, all from the nest that was still being observed at the end of the study and all heavily parasitized with botfly larvae (probably of the superfamily Muscoidea), grew atypically and are considered separately.

GROWTH AND DEVELOPMENT

General development.—At hatching the nestlings were naked, with yellowish red skin through which the viscera were easily observed. The legs were yellow, the bill was dull yellow, and a black egg tooth was present on the upper mandible. By day 5 of the nestling period the dorsal skin surface was dark brown and the ventral skin surface was yellow. By day 10 the egg tooth had disappeared and by day 13 the dorsal skin surface was greenish brown. By fledging at day 22 or 23, the exposed skin of the dorsal surface was red-tinged greenish brown, and the unfeathered portion of the ventral surface was yellow. The bill and legs were also yellow.

The eyes began to open on day 5 or 6 and were fully open one day later. Eyes open at a younger age in Beechey Jays than in Piñon Jays (days 7–9, Bateman and Balda 1973) and within the range reported for Florida Scrub Jays (days 4–7, Woolfenden 1978).

At hatching the nestlings gave soft squeaks and extended their necks

TABLE 1

CHANGES IN WEIGHT AND LENGTHS OF PRIMARY 9 AND RECTRIX 1 FOR NESTLING BEECHEY JAYS

Age[a]	Wt.[b]	P9[c]	R1[d]	Age	Wt.	P9	R1
1	12.2			12	110.5	25.8	4.0
	1.9	—	—		17.2	2.2	1.3
	9–14				78–128	23–28	3–6
2	17.8			13	116.2	29.8	6.8
	2.8	—	—		18.6	2.4	2.2
	14–21				84–131	26–32	5–10
3	23.5			14	120.0	33.7	10.3
	3.9	—	—		16.6	2.6	2.4
	18–27				88–135	30–37	7–14
4	32.5			15	122.3	38.8	13.8
	4.1	—	—		17.0	2.8	3.2
	26–37				90–139	35–42	9–19
5	41.7	1.6		16	123.3	42.5	17.8
	5.5	0.5	—		19.0	2.9	3.3
	34–47	0–2			88–140	38–45	13–23
6	53.3	2.8		17	124.0	45.8	21.8
	8.6	0.6	—		20.1	3.3	4.7
	40–62	2–3.5			86–142	40–49.5	15–29
7	63.7	4.3		18	125.3	49.3	25.3
	11.5	0.8	—		21.3	3.2	5.8
	45–74	3–5			87–141	44–53	17–35
8	75.0	7.3		19	125.7	52.7	29.8
	10.7	1.4	—		20.8	3.2	6.1
	66–86	5–9			89–142	47–56	21–40
9	85.7	11.7	0.8	20	128.5	55.2	33.2
	12.7	1.8	0.3		21.4	3.5	7.3
	64–98	9–13	0–1		87–143	49–59	23–45
10	94.7	16.1	1.7	21	130.7	58.3	37.5
	13.6	1.6	0.7		18.8	4.1	9.1
	71–111	14–17.5	1–2.5		95–145	51–63	23–51
11	104.2	20.7	2.3	22	129.4	59.6	43.6
	14.0	1.9	0.6		20.1	4.3	10.1
	80–122	18–23	1.5–3		96–143	53–65	30–58

[a] Age in days since hatching; hatch date = day 0; N = 6 for all days except days 13 and 22, when N = 5.
[b] Mean weight (g) (top number); SD (middle number); range (bottom number).
[c] Mean length (mm) of primary 9 (top number); SD (middle number); range (bottom number).
[d] Mean length (mm) of rectrix 1 (top number); SD (middle number); range (bottom number).

vertically to beg. By day 9 they were able to grasp objects (nest lining, fingers, etc.) with their feet. They were able to stand and move about the nest by day 13. By day 16 they made well-coordinated flapping motions with their wings and hopped around when placed on the ground. By day 18 they were able to perch and just prior to fledging (day 21 or 22) they made short hop-fly journeys into the branches around the nest.

Feather development.—At hatching the feather tracts were evident under the skin as areas of small dark dots. All juvenal primary, secondary, and alular feathers had broken through the skin by day 5 (Table 1, Fig. 1). The alar tract of Piñon Jays (Bateman and Balda 1973) and Florida Scrub Jays (Woolfenden 1978) erupted on day 4. Beechey Jays' capital, humeral, ventral, spinal, and femoral tracts were first evident as blue-gray quills less than 0.5 mm long on day 8. The rectrices erupted on day 9 (Table 1, Fig. 1). Rectrices erupted on day 5 for Piñon Jays and day 9 for Florida Scrub Jays. The crural tract was also first evident on day 9. The first feathers to break through their sheaths were in the alar tract, which did so on day 11 (usually about day 9 for Florida Scrub Jays). Feathers broke through the sheaths by day 13 for all other tracts except the caudal (day 14), humeral (day 15), and capital (day 17). Feathers of the ventral tract were completely free from their sheaths by day 17, femoral and crural feathers by day 18, and humeral and spinal ones by day 19. At fledging the feathers of the capital, alar, and caudal tracts were still partially sheathed. Beechey Jays were well feathered 3–4 days prior to fledging.

Weight.—The mean dimensions of 19 eggs measured at the Western Foundation of Vertebrate Zoology, Los Angeles, California, were 32.2 (SD = ±1.1) × 23.0 (SD = ±0.6) mm. The mean weight of 5 eggs, all laid in the same nest and all 12–13 days old was 11.2 g (range = 11.0–12.0 g). Each of these eggs weighed on the average 5.8% of the weight of an adult female ($\bar{x}$ = 194.0 g, N = 9). While this value is similar to those for fresh egg weights of Florida Scrub Jays (7.6%) and Piñon Jays (6.4%), weight lost by the Beechey Jay eggs during the almost 2-week period between laying and the date weighed may make the result artificially low. The eggs of Black-throated Magpie-Jays (*Calocitta colliei*) lost on the average 2.0 g between laying and 14 days of age (Winterstein, unpubl.). Assuming Beechey Jay eggs lost weight similarly (the two species are similar in adult weight and are sympatric), a fresh egg weight of about 13.2 g can be projected. This projected value is 6.8% of the weight of an adult female, within the range for Florida Scrub Jays and Piñon Jays.

Three hatchlings on day 0 had a mean body weight of 8.6 g, 4.4% of adult weight, a value smaller than the 6.0% figure given for Piñon Jays (Bateman and Balda 1973) and Florida Scrub Jays (Woolfenden 1978). This

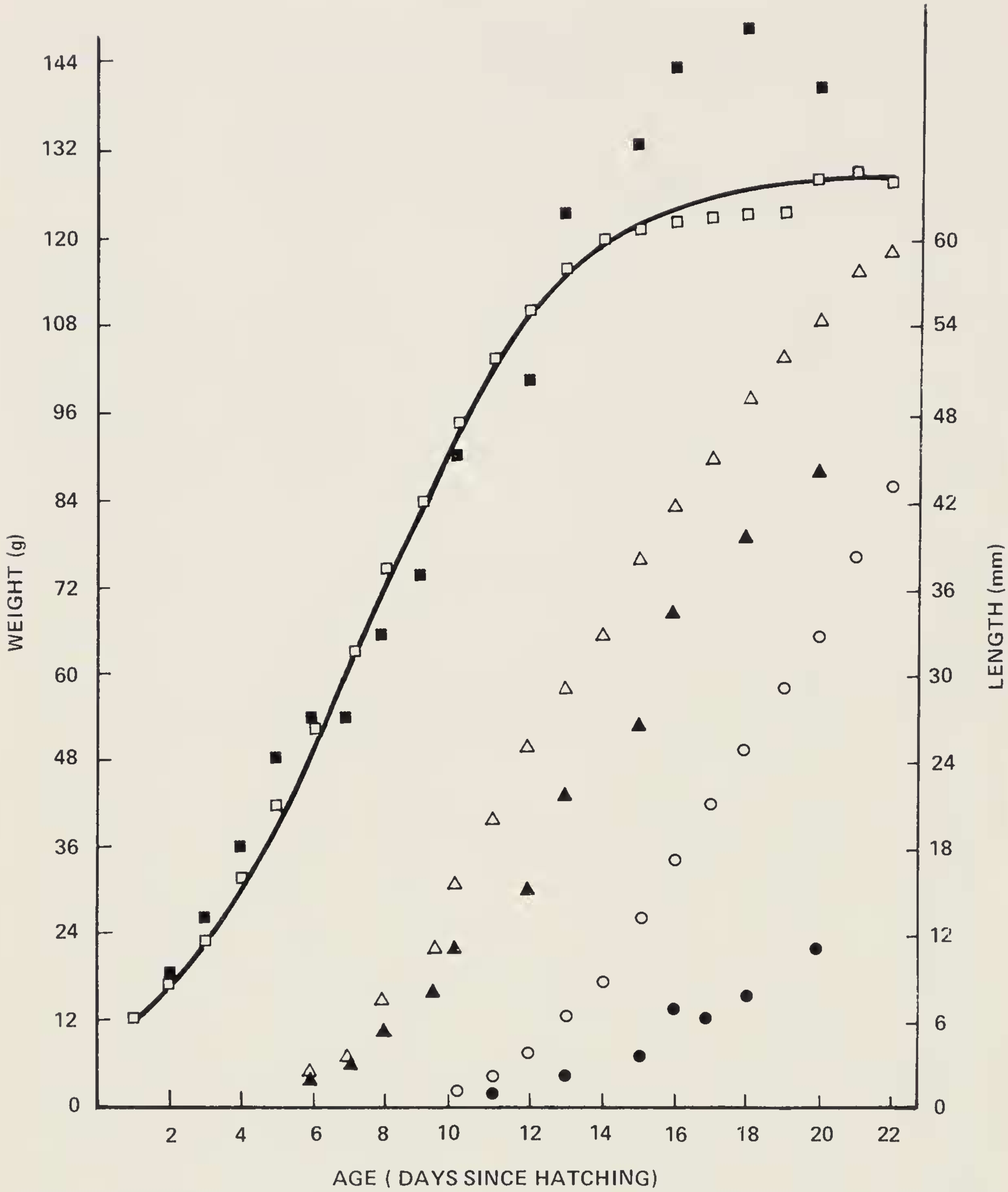

FIG. 1. Changes in body weight and lengths of primary 9 and rectrix 1 of nestling Beechey Jays. Open symbols indicate nestlings not infected with botfly larvae. For these nestlings N = 6 for all days except days 13 and 22, when N = 5 and the values plotted are the mean daily values listed in Table 1. Closed symbols indicate nestlings that were infected with botfly larvae. For these nestlings N = 3 for all days except day 20, when N = 2. Squares are mean daily weights; triangles, mean daily lengths of primary 9; and circles, mean daily lengths of rectrix 1. The line represents the growth curve fitted by the equation given in the text. Hatch date = day 0.

lesser value is not due to a substantially lower hatchling weight (Piñon Jay = 6.3 g, Florida Scrub Jay = 4.8 g), but rather to a much greater adult weight (Beechey Jay = 193.3 g, male and female weights $t = 0.08$, N = 18, NS; Piñon Jay = 103.3 g; Florida Scrub Jay males = 81.7 g and females = 76.7 g).

Weight increased rapidly from hatching until day 13, at which age the rate of increase declined markedly (Table 1, Fig. 1). Additionally, from day 16–19 the mean weights fell below those predicted by the growth curve (Fig. 1). Reduction in the growth rate during the second half of the nestling period may have been related to: (1) a decrease in integument weight as flight feathers became increasingly free of their sheaths and contained less water (Ricklefs 1979); and/or (2) increased allotment of energy for temperature regulation (see Ricklefs 1969, Case 1978).

The procedure used to analyze growth was that of Ricklefs (1967), also used by Bateman and Balda (1973) and Woolfenden (1978). Ricklefs' method requires an accurate determination of the age at fledging for proper interpretation of the results. Five of the Beechey Jay nestlings included in this analysis fledged on day 23 and the sixth on day 22. From 1974–1977, the first 4 years of study of this population of Beechey Jays (Raitt and Hardy 1979, Raitt et al., unpubl.), the average age at fledging was 21.3 days (SD = ±1.5, range = 20–24 days). In this 4-year period, each nestling was handled only one time, for banding. The age of the nestlings at banding ranged from 15–21 days.

The growth curve (Fig. 1) was best described by the logistic equation:

$$W = \frac{A}{1 + e^{-K(t_w - t_0)}}$$

where W is the weight of the bird in grams at day t_w, A is the upper weight asymptote in grams approached by the nestling, e is the base of natural logarithms, K is a constant proportional to the specific rate of growth, and t_0 is the age in days at the point of inflection on the growth curve (Ricklefs 1967). For Beechey Jays A was 129.9 g (Piñon Jays, 78.9 g; Florida Scrub Jays, 60.0 g). The age at which half of A was attained (t_0) was 7.2 days (Piñon Jay, 7.6; Florida Scrub Jay, 8.2). For the Beechey Jay, K, the overall growth rate index, was 0.360; slightly higher than that for the Piñon Jay (0.328) and the Florida Scrub Jay (0.335), indicating that although it is a larger bird, the Beechey Jay grows at a faster rate as a nestling.

Another method of comparing growth rates is to determine the time required to grow from 10% to 90% (t_{10-90}) of A (Ricklefs 1967, 1968). Based on Ricklefs' equations for determining observed and expected t_{10-90}, Beechey Jays grew more rapidly than predicted (observed = 12.2 days, expected = 15.2 days), while Piñon Jays grew essentially as predicted (observed = 13.4 days, expected = 13.3 days), and Florida Scrub Jays grew slightly slower than predicted (observed = 13.1 days, expected = 12.3 days).

At fledging, Beechey Jays had attained on the average 67% of adult weight. This is less than for Piñon Jays, 79% (Bateman and Balda 1973), and Florida Scrub Jays, 76% (Woolfenden 1978). In fact, it is less than that listed for 53 of 56 passerines (Ricklefs 1968: Table 2, *R* value). Value of *R* (fledging-to-adult weight ratio) is related to the stage of development of the young at fledging; according to Ricklefs (1968), low *R* values are indicative of species in which adults forage on the ground and fledglings escape predators primarily by running. However, adult Beechey Jays seem to forage in trees as often as on the ground and the young remain in the trees after fledging. The unusually low *R* value observed for Beechey Jays indicates that much growth occurs after fledging.

EFFECTS OF BOTFLY PARASITISM

The brood of three nestlings still in the nest when the study ended were heavily parasitized by botfly larvae. We were unable to fully identify these larvae, but they are probably members of the superfamily Muscoidea. Raitt and Hardy (1976) found that Yucatan Jays (*Cyanocorax yucatanica*) were similarly parasitized by *Mydaea* sp. (Muscidae). The larvae in Beechey Jays formed subcutaneous cysts in all areas of the body, including the skin around the eyes, the corners of the bill, and the feet and toes. These parasites were first observed when the young were 6 days old. On that day, one nestling (BB) had five larvae, another (BL) had six, and the third (RL) had 11 (Table 2). (Little is known about the life history of the parasite and it was, therefore, unknown exactly how many days elapsed between infection and emergence.) Larvae were first evident on day 6, and healed sores on day 10, suggesting about a 5-day maturation period. Changes in the total number of parasites per nestling (Table 2) indicate that reinfection occurred throughout the nestling period. On the last day on which the nest was visited (day 20), BB had 10 parasites, RL had 14, and BL was dead beneath the nest.

Physiological and morphological events, such as the eruption of particular feather tracts or changes in skin color, occurred at the same age in the heavily parasitized nestlings as they occurred for noninfected nestlings. However, behavioral development appeared retarded. Noninfected nestlings could grasp objects with their feet on day 9; infected nestlings were unable to do so until day 15. Noninfected nestlings could stand and move about the nest on day 13, whereas the infected nestlings could not

TABLE 2
NUMBER OF BOTFLY LARVAE INFECTING THREE BEECHEY JAY NESTLINGS

Days since hatching	Nestlings BB	BL	RL
1–5	0	0	0
6	5	6	11
7	5	7	12
8	—[a]	—	13
9	11	14	19
10	17	19	19
11	—	—	—
12	14	18	11
13	15	17	14
14	—	—	—
15	12	17	15
16	10	13	18
17	—	—	—
18	11	9	16
19	—	—	—
20	10	**[b]	14

[a] No data were available for that day.
[b] Nestling found dead.

do so until day 19. The infected nestlings made flapping motions on day 19, a behavior first observed on day 16 in the noninfected ones. By day 18 the noninfected nestlings were able to perch and could hop around when placed on the ground. Infected nestlings were never able to perch, nor to hop when placed on the ground. By day 20 (the last day they were observed) the two surviving, parasitized nestlings could no longer support their heads or stand. They suffered from severe spasms that caused their bodies to shake continuously during the measurement period.

Mean daily values for the three growth parameters for infected and noninfected nestlings are plotted in Fig. 1. A modified Friedman rank test, with ranking within days-of-age to remove the effect of growth and a single-degree-of-freedom-contrast (Steel and Torrie 1960), was used to compare infected (N = 3) and noninfected (N = 6) nestlings. Daily weights for the infected nestlings were significantly higher than those for the noninfected ones for the period prior to infection, days 1–5 (Friedman Value, χ^2_r = 7.68, $P < 0.005$). On the initial day of infection, day 6, the mean weight of the infected nestlings (54.0 g) was almost identical to that of the non-infected ones (53.3 g). From day 7 until day 13 the weights of the infected nestlings did not differ from those of the noninfected ones (χ^2_r = 1.73, P

> 0.10). From day 13 to day 20 the weights of the infected nestlings, a combination of the actual weight of the nestling and the weight of its associated parasites, were significantly greater than those of the noninfected ones ($\chi^2_r = 17.6$, $P < 0.001$).

The lengths of primary 9 were about the same for both groups (Fig. 1) for days 5–7, but after day 7 those of the noninfected nestlings were significantly greater than those of the infected ones ($\chi^2_r = 36.8$, $P < 0.001$). The lengths of rectrix 1 of the infected nestlings were significantly shorter than those of the noninfected ones throughout the observation period (Fig. 1; $\chi^2_r = 48.0$, $P < 0.001$). As the nestling period progressed, presumably a larger portion of the nutrients used in the development of feathers (and other morphological features) was lost to the parasites, causing these significantly reduced lengths.

On day 20, one nestling, BL, was found dead on the ground a few meters from the nest. Although the exact cause of death was not known, we suspect that it died as a result of being parasitized. The only obvious external injuries were the sores from emerged or still developing larvae.

As demonstrated, heavy botfly infestation of three nestlings retarded growth and development and probably caused death. However, when all (1976–1978, including Raitt and Hardy, unpubl. data) infected nestlings, regardless of parasite load (N = 19), were compared to all noninfected ones (N = 21), no difference existed in the number of nestlings that survived to one year of age ($\chi^2 = 0.15$, df = 1, $P > 0.50$). The deleterious effects of parasites on survival may have been obscured by the fairly small sample available and the small probability of any fledgling surviving to one year (38%, Raitt et al., unpubl.).

DISCUSSION

The growth and development patterns of Beechey Jays are atypical for passerines of their size and for social jays studied thus far. Because of their much larger size Beechey Jays would be expected to grow slower than Piñon Jays and Florida Scrub Jays; however, the opposite is true. At fledging Beechey Jays are only 67% of adult weight, while most passerines are between 80 and 100% (Ricklefs 1968: Table 2) and Piñon Jays and Florida Scrub Jays are both above 75%. Also, the Beechey Jay's nestling period (22–23 days) should be longer (see Ricklefs 1968, 1979) than that for Piñon Jays (21–22 days; Bateman and Balda 1973), which it equals, and Florida Scrub Jays (17–18 days; Woolfenden 1978), which it slightly exceeds.

The observed growth rate, fledging-to-adult weight ratio, and pattern of development may be adaptations to facilitate breeding in a highly seasonal environment. Complex interactions of food supply and predation pressure, which are related to the very distinct wet and dry seasons, may have influenced both the time of year when Beechey Jays breed and the duration of their nesting period.

For Beechey Jays, as for most birds (Lack 1968), food supply is probably the ultimate factor most important in influencing the initiation of breeding. Young Beechey Jays generally hatch during the dry season-wet season transition period and fledge soon after the wet season begins (Raitt and Hardy 1979). Moffitt (1980) found that insect numbers on the study site were lowest just prior to the first rains, increased steadily throughout the wet season, and then began to decline steadily when the rains stopped. As insects are the primary food items fed to the young, Beechey Jays cannot profitably initiate breeding any earlier in the year.

Food supply, however, is insufficient to explain why Beechey Jays do not delay breeding until later in the wet season when food is plentiful, or why the young fledge at such an early stage in development. We hypothesize that predation, which accounts for the majority of nestling losses (78%, Raitt et al., unpubl.), is the factor preventing adult Beechey Jays from delaying the onset of breeding and nestlings from remaining longer in the nest. Beechey Jays protect their nest by cooperatively mobbing predators, which they locate primarily by sight. We postulate that after the wet season begins, nests become progressively harder to defend; under the cover of the dense, green foliage, predators presumably can get closer to the nest without being detected. After fledging, the young are fairly mobile and can be hidden quite well in the same foliage that offers cover to predators. Therefore, fledging the young as soon as possible after the wet season begins, reduces losses to predators. Calculated by the Mayfield method (1961, 1975) (and see Winterstein 1980), the probability of producing a fledgling from an egg laid in an early nest (young hatched before the wet season began) was 31%, while that of an egg laid in a late nest (young hatched after the wet season began) was only 17%; the difference was caused entirely by nestlings of late attempts having only one-third the survival probability of those of early attempts. The fact that nests may also become progressively harder for predators to find after the wet season begins may be offset by their ability to remember the location of a nest previously located, but not yet preyed upon.

Predation is not the only risk of remaining in the nest. Because the chances of botfly infection presumably increase as the time in the nest increases and the probability of reinfection certainly does (Table 2), reduction in the length of the nestling period also will reduce losses to parasites.

Shortening the nestling period will not in itself automatically result in an increase in the survival rate of the young; at fledging they must be mature enough to function out of the nest. The pattern of development must be such that when fledging occurs, functions necessary for survival out of the nest have reached at least some minimal level of development. To survive out of the nest Beechey Jays must have reasonably well-developed locomotor organs and neuromuscular control; in fact they apparently attain that stage of development as early as 2 days prior to fledging. Beechey Jay fledglings are fairly mobile and very inconspicuous shortly after they leave the nest. The fledglings are extremely difficult to locate. Despite extensive searching, only twice in 5 years did we find fledglings that had been out of the nest longer than 1 day, and we were able to follow them for no more than 2 successive days. The rapid development of locomotor organs and neuromuscular control apparently occurs at the expense of overall body weight. This pattern of development will increase the chances of young surviving only if there are no serious disadvantages associated with having a low body weight at fledging. We found that actual weight at fledging had little effect on subsequent survival. Those young that weighed less than the mean weight at fledging for this population were as likely to survive to yearling age as those that weighed more than the mean ($N = 54$, $\chi^2 = 1.06$, $df = 1$, $P > 0.25$) (see also Woolfenden 1978).

The role of mortality factors, including predation and parasitism, in the evolution of growth rates has been the subject of controversy (Ricklefs 1969, 1979; Case 1978). Based on his failure to find a correlation between reported juvenile mortality rates for particular species and the growth rates of these species, Ricklefs (1969:1032) argued that "specific differences in mortality rates are responsible for little, if any, of the observed diversity in growth rates" (but see Case 1978). The relationship we have postulated between predation-parasitism and growth rate in Beechey Jays might be construed as contrary to Ricklefs' findings. We believe, however, that this is not the case. For example, in a later paper Ricklefs (1976:198) stated that "early fledging must require rapid growth and maturation; both of these factors undoubtedly respond in parallel to variation in nest mortality rate." We have emphasized the shorter nestling period in Beechey Jays as an adaptation to reduce losses to predators and parasites, and that three adaptations combine to produce the shorter nestling period: rapid growth rate, development that results in relatively precocious locomotor abilities, and fledging at a relatively low body weight.

The above mentioned adaptations may be dependent upon the fact that Beechey Jays are cooperative breeders. The number of helpers at a nest is significantly related to the rate at which the nestlings are fed (Raitt et al., unpubl.), suggesting that the rapid growth rate could be, at least partially, a function of the contributions of helpers (see Case 1978). However, our small sample of nestlings precludes rigorous testing of the relation between feeding rate and growth rate. Also, in the long postfledging developmental period (full development presumably is not attained until well into or near the end of the wet season), the young are undoubtedly dependent upon the cooperative efforts of all group members for food and protection. The long period of postfledging care presumably mitigates any disadvantages associated with having a low body weight at fledging (see Bateman and Balda 1973, Woolfenden 1978). These latter considerations are necessarily speculative; a definitive analysis of the overall effects of sociality on growth and development requires data on more solitary and cooperative breeders than have been studied to date.

SUMMARY

Nestling growth and development patterns were analyzed for a population of cooperatively breeding Beechey Jays (*Cyanocorax* [*Cissilopha*] *beecheii*) near Mazatlán, Sinaloa, México. Nestlings were found to have a faster growth rate (Ricklefs' K value = 0.360) and shorter nestling period (22–23 days) than would be predicted for jays of their large size. Locomotor organs apparently developed rapidly, at the expense of overall body weight. At fledging the young were only 67% of adult body weight, but very mobile and difficult to locate.

Three nestlings, heavily infected with subcutaneous larval parasites, grew atypically. Physiological and morphological stages were reached at the same age in both infected and noninfected nestlings, but behavioral capabilities in the infected group were retarded. Infected nestlings weighed more than the noninfected ones both prior to being parasitized (day 6) and after day 13 of the nestling period; between days 6 and 13 the weights of the two groups did not differ. Lengths of primary 9 and rectrix 1 of the parasitized nestlings were significantly shorter than those of fledging nonparasitized ones.

The rapid growth rate, low fledgling-to-adult weight ratio, and subsequent short nestling period of normal Beechey Jays are seen as adaptations to facilitate breeding in a highly seasonal environment. Limited food supply during the dry season and intense predation pressure and increased likelihood of being parasitized during the wet season preclude breeding at any time other than the late dry season-early wet season period and strongly select for the shortest nestling period possible. The rapid growth rate of nestlings and survival of fledglings may depend upon the cooperative efforts of all group members.

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